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No. 2.

Some Observations on the Morphology and Mechanism of the Parts in the Orthorrapha.

SINCE the discovery of the practical importance of the blood-sucking Diptera the attention of investigators has to a large extent been concentrated on the study of their binomics, distribution and classification, to the neglect of the problems which attracted the older entomologists, and the study of the homology of the parts and of the mechanism by which they act have received little attention. Much of this neglect is due, no doubt, to the fact that so large a proportion of the recent work has been done by medical men and others to whom entomology was of interest mainly as an applied science, and these problems, fascinating though they are to the zoologist, have no apparent connection with the rôle played by insects in the transmission of disease. It is not unnatural that such a restricted point of view should have led to misconceptions, and more especially since the mosquito, which, on account of its great economic importance, has been more studied than all the rest of the group together, happens to be a very highly specialised form. Moreover, most of the common mosquitoes are small and delicate flies, and are not at all easy to dissect, and it is not to be wondered at that many points in their anatomy and physiology should have been missed, when a comparative study was not attempted. In such a compact natural group as the Diptera, in which, although the variation in form is very great, the general principles of structure are maintained throughout, questions of the homology and of mechanism are intimately bound up with one another, and it is of the first importance to compare the separate parts in one fly with those, often markedly different in appearance, which fulfil the same function in the others. The comparative method, indeed, is not only the one by which the more strictly zoological side of the question is to be attacked, but it is of great assistance in elucidating the physiology of the proboscis, a matter of importance to the parasitologist.

I do not propose to attempt in the following pages any comprehensive review of the subject, not having at hand the necessary literature, but to discuss some of the more important points of structure and their bearing on the

mechanism of the proboscis. At the outset it will be well to emphaize the fact that the process by which a blood-sucking fly obtains blood from the host is essentially a mechanical one, in the sense that it is governed by the ordinary principles of muscle movement and of physics. Any explanation of the process which is not in accord with the anatomy of the parts, or which takes no account of ordinary physical laws, must be rejected. One may add, that any hypothesis which would attribute to an organ in one fly a function which it does not possess in another is to be regarded with suspicion, and that due regard is to be given to the observed habits of the insect, when the size of the fly and other circumstances permit of observation. A critical examination of the method of feeding with these points in mind will show that the subject is by no means so simple as at first appears, and that many of the statements current, especially with regard to the mosquito, are vague and inaccurate.

It will be convenient to discuss the subject in two parts, the making of the wound and the sucking up of the blood.

The Biting Apparatus and its Mechanism.

The biting apparatus in the orthorraphic flies is ordinarily described as consisting of the paired mandibles and maxillæ, the labrum-epipharynx, and the hypopharynx. The orthorraphic biting flies are sharply distinguished from those of the Muscid group by the fact that the labium does not enter into the wound at all, functioning mainly as a sheath for the other parts.

The first question which attracts one's attention is as to the nature and origin of the force by which the "piercing stylets" are driven into the skin of the host. Most accounts of the mouth parts of the mosquito simply state that the piercing parts are thrust into the skin, without attempting to explain how this is done, though Nuttall and Shipley go so far as to say that the mandibles enter the skin when the labrum is thrust in, by means of the "same elastic force which induces the sharpened end of a piece of whale-bone to pierce a soft body if the other end is pushed towards the surface," and they note the presence of muscles for the retraction and protrusion of the maxillæ. Annett, Dutton and Elliot state definitely that "the piercing of the skin is brought about by muscular force directed from the body of the insect, the muscles attached to the bases of the stylets serving to keep them rigid." Actual observation does not help us much in the case of any of these flies, for all the parts concerned are small and concealed by the labium. The position of the fly while in the act of feeding is, however, of some importance. If it were simply a question of *vis a tergo*, then one would expect that the piercing parts would be brought into line with the long axis of the body, for it is obvious that the muscles concerned would act at a great mechanical disadvantage if

they had to propagate a force through an angle. But this does not occur as a general rule. The only striking case in point is that of *Hæmatopota,* which when in the act of feeding raises the posterior part of the body so much that it makes with the surface of the skin an angle of nearly half a right angle. The posterior surface of the head and the anterior surface of the prothorax are moulded to fit one another, and, as the neck is a very short one, it is probable that some force at least can be propagated from the thorax, though not, it should be noted, through the neck. But even in this case it is improbable that the force from behind enters largely into the mechanism, for in *Tabanus* and the allied genera, although the mouth parts are almost identical, the position assumed by the fly is such that the body is parallel with the skin and the proboscis perpendicular to it. *Ceratopogon* assumes a position similar to that of *Hæmatopota,* but as the proboscis is perpendicular to the long axis of the body the manœuvre cannot possibly bring the two into the same straight line. In *Anopheles* the proboscis is directed straight forwards in the position of rest, and to reach the skin at all the insect has to raise the hind end of the body and to depress the proboscis, thus doing away with the apparent advantage of its attitude; as a matter of fact the proboscis is bent downwards very nearly to a right angle, as shown in Nuttal and Shipley's admirable drawing.

The attitude assumed by the fly when feeding therefore renders the operation of a force propagated from the thorax unlikely. We have next to consider how far the anatomical arrangements are adapted for such a force. So far as the muscles are concerned the question is a simple one. In all cases the feet are provided with claws admirably adapted to enable the fly to take a firm hold on the skin, and it might be supposed that the extension of the joints of the middle and hind legs would result in a forward thrust of the thorax and head of the fly. The ends of the piercing organs being then applied to the skin, they must enter or else bend forward, and we know that the latter, at least in the case of the mosquito, where the piercing stylets are readily seen when they are separated from the retracted labium, does not occur: in any case mere bending would not be of advantage, unless we adopt the view noted above for the mandibles, that the potential force produced by their flexion is used up in piercing the skin. A moment's consideration will show that this explanation will not suffice, either for the mandibles alone or for the piercing parts as a whole, for it would follow that the cutting edges of the blades must be directed forwards, while as a matter of fact those stylets which have cutting edges at all have them directed in the lateral plane.

Bending and elastic rebound are therefore out of the question for any of the mouth parts. There remains the simple thrust, which is rendered unlikely by the attitude of the fly. But a forward thrust cannot be propagated without

some rigid structure through which it can act, and in this case the necessary rigidity would have to be ensured by the neck. As a matter of fact the neck of these flies is not at all adapted for such a purpose. Its length varies a good deal in the different forms, being very short in the *Tabanidæ*, and comparatively long in the mosquito. But in no case does it possess an amount of rigidity sufficient to permit of the propagation of a force capable of driving the stylets into the skin. By far the greatest portion of the wall of the neck consists of a soft and flexible membrane, attached in front to the borders of the occipital foramen and behind to the opening into the thorax. In this there are developed thin plates of chitin, one on each side, usually free from one another, but approaching in the middle line ventrally. These cervical sclerites are loosely articulated with the epicranium in front, but in none of the species which I have examined do they take part in a definite articulation with the thorax. In the *Tabanidæ* the cervical sclerites are displaced backwards out of the neck, and are found at the sides of the thoracic inlet, two of the three pairs being entirely free from chitinous attachments. The cervical sclerites, in fact, are mere strengthenings of the integument of the neck, and fill no other functions than those of affording additional support in the cases where the neck is long, and of providing attachments for the muscles which move the head. The neck is a soft canal, capable of distension as blood flows through the œsophagus, a point well shown in Nuttall and Shipley's drawing of the mosquito in the act of feeding.

The motive force must then lie in the head or the neck. The latter may be disposed of in a word or two. The muscles it contains are very small, and are merely the representatives in this region of the fibres which connect adjacent segments elsewhere in the insect body. Their function can be no more than to move the head on the neck, the looseness of the membraneous wall permitting of a certain amount of retraction and rotation, easily seen when a mosquito is beginning to feed and is searching for a suitable spot for the puncture. It is impossible to conceive of any arrangement of muscles by which the neck could be extended in such a way as to drive the mouth parts into the wound, nor can any such muscles be found by section or dissection.

The argument brings us to the conclusion that the muscles which make the wound are situated in the head of the fly. Before going further it will be well to consider for a moment the origin of the several organs ordinarily described as the piercing stylets. The *labrum-epipharynx* (Text-figure 2, page 27) is the result of the fusion of the labrum, which is an extension downwards of the clypeus, and in other insects connected with it by a freely moveable joint enabling it to act as a true upper lip, with the epipharynx, an outgrowth of the stomodæum, and in these flies easily traced upwards to its

termination in the first part of the sucking apparatus. The fusion between them is not so close that the two become welded into one organ, for the epipharynx in all forms retains the shape of a nearly closed canal; the labrum may, as in the mosquito, adapt itself to the shape of the epipharynx, or it may remain flattened and blade-like. There is in all the forms which I have examined evidence of a joint between the labrum and the clypeus, at the situation of the corresponding joint in insects such as the cockroach, which have a freely moveable upper lip, and in the region of this joint the labrum and epipharynx are much less firmly united than elsewhere. The *hypopharynx* is usually described as an outgrowth from the lower lamina of the stomodæum, corresponding to the epipharynx, but it would be more accurate to describe it as consisting of two laminæ, the upper one of which is derived from the stomodæum, the lower from the labium, the two enclosing between them the salivary duct. The distinction between the two laminæ can be made out by dissection in the larger *Tabanidæ*, in which it is quite easy to pull away the lower lamina still attached to the base of labium, and to leave the upper lamina, along with the salivary duct, still attached to the first sucking chamber. In all these biting flies, which must of necessity introduce the saliva into the wound, the lower lamina of the hypopharynx is completely separated from the labium, but in very nearly allied forms, and even in the males which do not suck blood, as in the case of the mosquito, the lower lamina remains attached to the labium. The separation is evidently due merely to the necessity of introducing the saliva into a comparatively deep wound, into which the labium does not enter.

The *mandibles* (Text-figure 1, page 13) represent the appendages of the fourth segment of the insect head, and are homologous with those of other insects, such as the beetles, in which they act as cutting and tearing weapons. Similarly the *maxillæ* correspond to the appendages bearing the same name, but with much more obvious functions, in other arthropods. They are the only appendages in the *Nematocera* which retain at all closely the primitive form.

Now, to repeat the statement made in the opening paragraph, we should regard with suspicion the supposed function of the labrum-epipharynx and hypopharynx as piercing organs, if for no other reason that they are homologous with structures which do not ordinarily possess such a function, whereas we would confidently expect the mandibles and maxillæ to play a prominent part in the making of the wound. It is now necessary to examine the musculature and armature of these organs, to see how far they are consistent with this view.

There is only one muscle attached to the labrum-epipharynx, and this is found in the same place as that which in the cockroach lifts up the upper lip.

It is conspicuous in *Tabanus*, in which it has been figured by Meinert and Hansen, and occurs also in the mosquito, and is very clearly shown in Nuttall and Shipley's drawings. It lies immediately behind the articulation between the labrum and the clypeus, arising from the internal surface of the latter and finding attachment to the proximal extremity of the labrum at the point where it is only loosely attached to the epipharynx; it is difficult to decide its exact point of insertion, or its function. Meinert regarded it as a depressor in *Tabanus*, while Nuttall and Shipley describe it in *Anopheles* as an elevator. Whatever its function may be, one thing is clear, that it cannot act as an extensor of the labrum. It is of constant occurrence in the Nematocera.

The hypopharynx has no muscle attached directly to it, so we have to pass further back, to the sucking chambers to which the epipharynx and the hypopharynx are so intimately attached. Here we find another proof, incidentally, that the forward thrust of the body of the fly cannot act as a motive power, as far as these two organs are concerned, for in no member of the group is there any chitinous connection between the wall of the head capsule and the sucking apparatus. Force transmitted to the head from behind can only be propagated to the labrum, and through it to the epipharynx by the attachment of the labrum to the clypeus, and to the hypopharynx by means of its loose basal attachment at the proximal end of the labium. There are, however, certain muscles attached to the sucking chambers which undoubtedly have the power of raising and lowering them, and with them the stylets which arise from them. These muscles can only be made out as definite bundles in *Tabanus*, in which they have been figured by Meinert. There are two sets, one of which is inserted at the upper end of the first sucking chamber, and by pulling in an upward direction retracts the chamber and with it the labrum-epipharynx and hypopharynx; the second set are attached about the same place but pull in a downward direction, and will therefore thrust the stylets into the wound. In *Simulium* the retractor muscles are present, as figured by Meinert, but the protractors do not exist as a distinct bundle. In *Anopheles* the first sucking chamber is a very small one, and the protractor and retractor muscles are not distinguishable. It is possible that some of the fibres of the muscle termed by Nuttall and Shipley the elevator of the palate may act as protractors and retractors to a slight extent.

Whatever be the true function of these muscles it is evident that they are not essential to the act of insertion of the proboscis, for they do not occur in an equal degree of development throughout the group, and are not to be distinguished in the mosquito, the piercing apparatus of which is at least as efficient as that of any of the other flies. In any case, it is almost inconceivable that

such small muscles, acting at such a manifest disadvantage, could drive the labrum-epipharynx into the skin, even in the case of *Tabanus*. The extent of their action in protracting and retracting the labrum-epipharynx is limited to the amount of bending which can take place in the labrum at that portion of its upper end which is only loosely attached to the epipharynx. The utmost capacity of the protractor muscles can only suffice to stretch the proximal end of the labrum until it is in the same straight line as and in contact with the epipharynx. The amount of retraction is less easy to define, for it is limited only by the loose joint between the labrum and the clypeus, and there is nothing to prevent the first chamber, which in all cases is connected to the second by a membraneous canal, from being drawn up within the head, except the muscles which support it and connect it with the wall of the head capsule. It will be necessary to refer to this point later on, but for the present it will be sufficient to state, that the anatomy of the parts indicates that though a certain amount of retraction and protraction of the first sucking chamber can take place, the action is not a powerful one, and the limit of extension is such that the distal ends of the labrum-epipharynx and hypopharynx cannot extend further than the level of the ends of the mandibles and maxillæ. The fact that protractor and retractor muscles cannot be distinguished in the highly efficient mouth parts of the mosquito is a strong argument against their taking any prominent part in the making of the wound in the closely allied flies.

One other point occurs to one in this connection. No matter what the armature of the tip of the labrum-epipharynx may be, and as will be shown later it is ill adapted for piercing, it would work at a very great mechanical disadvantage if actuated by a simple forward thrust, without any lateral movement or rotation. If one attempted to drive a carpenter's augur through a piece of wood without the usual rotatory movement, the amount of force required would be infinitely greater than it normally is. Rotation of the labrum-epipharynx and hypopharynx is of course anatomically impossible.

It will be convenient to sum up the argument at this point. The driving force by which the piercing parts are inserted into the skin is not derived from the muscles of the legs or thorax, because the neck is too flexible and slender to transmit such a force. It is not to be found in the muscles of the neck, for these are sufficient only to move the head on the thorax in the adjustment of the proboscis to a position favourable for feeding, and there is no arrangement by which the neck could be forcibly extended so as to drive the stylets into the skin. The position of the proboscis in relation to the long axis of the body is a most unfavourable one for the exercise of any thrust from behind, as such a thrust would tend to bend the proboscis backwards towards the thorax.

The ingenious suggestion of Nuttall and Shipley that the mandibles enter the skin by means of an elastic rebound from a bent position will not hold for either the mandibles or the other stylets, for the cutting edges are invariably directed laterally, and moreover in most of these forms the stylets are flattened from side to side. The labrum-epipharynx and hypopharynx are capable of a certain amount of protraction and retraction, but the movement of protraction is limited to the amount necessary to bring their distal ends to the level of the tipe of the mandibles and maxillæ, and is in any case not a powerful movement, nor does it occur with such uniformity, at least as regards the degree of development of the muscles concerned, that one is justified in regarding it as an essential factor in the making of the wound.

There remain for consideration the mandibles and maxillæ, true appendages, homologous with those which are used by other arthropods to obtain their food, and those which, on general zoological principles, one would expect to find functioning as cutting organs.

In the mouth parts of insects there are many wonderful contrivances elaborated by nature to achieve her end, but nothing more remarkable than the adaptation of these appendages to their present function. Throughout the group, notwithstanding the individual variations, the mandibles and maxillæ preserve their distinctive character in such a way that one can readily discern in them the resemblance to the cutting and clasping appendages from which they have originated. So close is the resemblance that a general description will apply to any of the forms in the group. The mandibles are flattened and blade-like, terminating in a sharp point, slightly recurved after the manner of a sabre, and armed on the inner edge of the blade with a single row of fine serrations strikingly like those on the edge of a saw. The two mandibles are in the same plane, their inner edges being directed towards one another and almost meeting in the middle line in the position of rest. At the base of the blade the mandible is articulated to the edge of the gena, in a position corresponding to the ginglymus in other insects, and the articulation is such as to permit of an inward and outward movement of the blade, on the pivot formed by the point of attachment. This is very well shown in the larger *Tabanidæ*. The base of the mandible in these forms divides into a pair of stout cornua, the external one of which is articulated to the gena, the internal one free. To each of these cornua muscles are attached, by the contraction of which the mandible is alternately rotated inwards and outwards on its pivot, the muscles attached to the internal cornu acting as adductors of the blade, those attached to the external one as abductors. Now the cutting edge is internal, and this edge is not straight, but curved outwards, so that the motion of adduction does not merely displace the cutting edge inwards, but draws it obliquely through

the wound almost at the angle at which one ordinarily uses a knife. The action is very like that of a circular saw acting through a short arc.

With the exception of the mosquitoes, all the members of this group have well developed mandibles, and the variation found in the different forms is remarkably small. In *Tabanus* (figure 4) the serrations are extremely fine, although the blade itself and the edge bearing the serrations are quite strong. In *Simulium* (figure 2) the serrations are much larger and are continued round the tip of the blade to the external border. In *Ceratapogon* (figure 3) they are intermediate in size, and the inner edge of the blade is bent rather abruptly outwards, so that the teeth are directed inwards and forwards, and the point of the blade a blunt one.

In *Phlebotomus* the serrations are a little coarser than those of *Tabanus*, and are more widely separated; the blade is flattened. Newstead states that it is the outer edge which bears the serrations. I have not had the opportunity of making a sufficiently large number of preparations to express an opinion on the point, nor have I been able to consult Grassi's paper on this fly, though, thanks to the kindness of Dr. Ashmorth, I have obtained a copy of his drawings. In these I note that he represents, in a cross section of the proboscis, that the mandibles lie superimposed upon one another between the labrum-epipharynx and the hypopharynx, a most remarkable position for them to occupy, for they render it impossible for these two structures to form a closed food canal. Newstead, who offers no remark on this point, gives a drawing of the labrum-epipharynx and hypopharynx in apposition with one another, without showing the mandibles between them. Great difficulty arises in decided points such as these on account of the small size of the parts and the impossibility of separating the component parts of the proboscis without injuring some of them. In many of my preparations of *Ceratapogon* the serrated edge of the mandible appears to be external, and is in fact external to the edge of the labrum-epipharynx, but this is due to the two mandibles having crossed one another, and what appears to be the external edge of the mandible of the left side is really the internal edge of the one on the right. As already explained the direction of movement of the mandible is inwards and outwards in the lateral plane, and although there is no proof that they normally pass beyond the middle line, there is no reason, anatomical or otherwise, why they should not do so.

The *Culicidæ* show a certain amount of variation in the mandibles and it looks as if they were tending to disappear in that family. On account of the great elongation of the parts in the mosquito the cutting portion of the blade is limited to the distal end, which is slightly expanded. The serrations in *Anopheles* (figure 5) are excessively minute, and can only just be made out

with a magnification of a thousand diameters, and in *Culex* it is difficult to be sure that they exist at all, nor is it possible in either case to say whether the serrations are on the outer or the inner side. In the male mosquito the whole appendage is missing. The muscles at the base of the mandible are not recognisible in this form, and one is justified in assuming that the appendage is of much less importance in the mosquito than in the other families. It would be interesting to know if the gradual disappearance of the mandible goes on *pari passu* with other changes in the different genera, and if there are any blood-sucking species in which the female is without mandibles.

The *maxillæ* are even more admirably adapted for the purpose of making a wound than the mandibles. The most remarkable feature about these appendages is the manner in which the primitive arrangement of the joints is maintained. The maxilla of a primitive insect, such as the cockroach, consists of five parts, the lacinia, galea, and palp, external organs, named from within outwards, and the stipes and cardo which are internal. Of these the palp persists and retains its sensory character throughout the Diptera; the galea becomes the cutting blade in the Nematocerous biting flies and the lacinia remains only as a small peg shaped projection at the base of the blade on the inner side. The stipes appears in these forms as a backward continuation of the blade, and passes through the interior of the head cavity in its lower part, external to and below the first part of the sucking apparatus, to a point almost as far back as the occipital foramen. Here it is attached to the wall of the head cavity by the interposition of the cardo, which is always very small and in the case of the smaller and more delicate flies may be absent. The maxilla is capable of movement on the joints between the stipes and the cardo, and between the cardo and the wall of the head capsule, into a small notch in which the cardo is fitted.

This arrangement is best studied in the large *Tabanidæ*. Here the cardo is easily seen as a wedge-shaped rod articulated in a small notch at the edge of the space occupied by the palatal membrane, and the method of action can be readily understood by an examination of the muscles which are attached to the stipes and cardo. As in the case of the mandible, there are two sets, termed by Meinert the adductor and abductor; the former arise from the internal surface of the head capsule near the occipital foramen, and run directly forwards in line with the stipes; the latter run in the opposite direction, arising from the anterior wall of the head capsule in the region of the gena, and are inserted into the cardo. The two sets are therefore antagonistic, and act on the joint between the stipes and the cardo, and on that between the cardo and the wall of the head, in opposite directions. The adductors would be more accurately described as retractors, and the abductors as protectors, for the

action of these muscles must be to alternately protract and retract the stipes, and with it the cutting blade.

The armature of the maxillæ presents both a remarkable uniformity in all the flies included in the group, and a remarkable adaptation to the method of action of the muscles. In all cases the type is that of a rasp, on which most of the teeth are directed backwards, so that it cuts mainly when it is retracted. The cutting edge may be on the inner or the outer side, or both edges may be armed; the blade may be straight or a little curved.

Before going further the individual variations in the maxillæ may be noted. In the *Tabanidæ* (figure 10) the blade is stout and roughly quadrilateral, and is armed all round the distal end with strong spines which are only slightly raised from the surface of the blade; these spines are continued a considerable distance down the internal border, but only for a short distance externally. On the external border there is a row of extremely fine and closely set hair-like spines, the distal ones of which are enlarged basally to form regular spines like those on a rose tree. The blade is almost straight from apex to base, and is continued directly into the stipes. In *Simulium* (figure 1) the blade is flattened and triangular, and has down each side a single row of spines similar to those of *Tabanus*, but smaller. In *Ceratapogon* (figure 8) the blade is flattened and at the base is thicker on the external side than internally. Towards the apex the inner side becomes attenuated to a very thin and almost invisible edge, and the blade itself is twisted transversely, so the terminal portion of the internal edge is directed outwards. This terminal portion is armed with a row of extremely minute backwardly directed spines, set on the fine internal edge and somewhat widely separated from one another. In *Phlebotomus* (figure 12) the blade is similarly flattened and bent transversely,* but in this case both edges bear teeth. On one side there are six, all directed backwards and extending to the extreme tip, and on the other a row of very much smaller ones, not extending to the distal end, and directed upwards. In mosquitoes the blade is flattened and very much elongated. The inner side of the blade is thickened to a prominent ridge from the base and upwards, and the external edge is very thin and sharp, so that on cross-section the blade has a triangular outline. In cleared preparations the distal portion of the blade is usually bent outwards, but this is probably an artifact due to the different amounts of shrinkage in the thick and the thin edges. The blade is produced to a fine point, and in some cases, especially in the smaller forms such as *Anopheles maculipennis*, figured by Nuttall and Shipley and in

* The transverse bend may be an artifact.

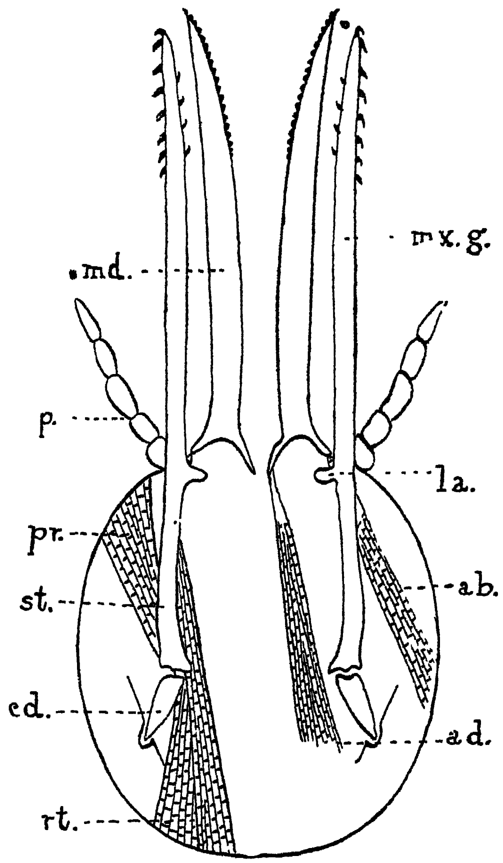
Culex fatigans, is slightly expanded. On this portion there is a single row of minute thorn-like teeth, all projecting backwards. In a large species of *Joblotia* (figure 3) I have seen a much more complex arrangement. The blade is the same as in the smaller forms, but at the tip it is armed on both sides. On the external side there are five comparatively large teeth, similar to those of the smaller mosquitoes. The distal one of these is situated some little distance from the pointed tip of the blade, and in the interval there are two much more delicate teeth with very sharp points, which point in the opposite direction to those above them, that is, towards the tip of the blade. On the internal edge there is a single row of short but stout teeth, seven in number, resembling those of *Tabanus*, and extending around the edge on to the two surfaces of the blade.

The stipes is readily seen in all these flies in cleared preparations of the head, as a stout rod running across the floor of the head cavity. It has been described in *Tabanus, Anopheles,* and *Phlebotomus*, in the latter two as the "apodeme" of the maxilla, and it presents very much the same appearance in *Simulium* and *Ceretapagon.* The cardo is less easy to distinguish on account of its small size, and I have not succeeded in distinguishing it in small species. In *Culex concolor* and in *Joblotia* it can be made out as a distinct piece at the base of the stipes. Its existence is not of course necessary for the mechanism of the maxilla, as it would suffice if the stipes were connected to the wall of the head capsule by the fibrous tissue, and I am inclined to think that this is the case in many forms, for one notices that the stipes remains adherent to the chitinuous wall in cleared preparations.

The muscles which act on these joints to produce the protraction and retraction are arranged in the same manner throughout, though it is a matter of some difficulty to make out their precise insertions in the smaller species. They are always to be found in transverse sections of the head, and I have found them in this manner in *Ceratapogon* after failing to dissect them. There is no doubt of the existence of a relatively large bundle of muscle fibres surrounding the stipes in all case, though one cannot always differentiate between the adductors and the abductors. The arrangement depicted by Nuttall and Shipley in *Anopheles maculipennis* is found also in *Joblotia* and *Culex concolor*.

The mode of action of the maxilla will now be evident. The extreme tip of the blade is pushed into the skin by the protractor muscles, and meets with very little resistance on account of the fineness of the point and the upward direction of the spines. It is then withdrawn by the retractor muscles, and as this takes place the rasps catch against the tissues and lacerate them.

Protraction and retraction follow one another rapidly, and each time the barbs are drawn upwards through the wound they enlarge it, so that at the next protrac-



TEXT FIGURE 1.

Diagram of the mandibles and maxillæ of the orthorraphic biting flies.

md., mandible.
ab., abductor muscle of the mandible, ad., its adductor.
mx. g., the galea, (the cutting portion) of the maxilla.
la., the lacinia.

p., the palp.
st., the stipes.
cd., the cardo.
pr., the protector muscle.
rt., the retractor.

tion the tip of the maxilla can penetrate, still against little or no resistance, further into the wound. When a certain depth is reached, the teeth on the opposite side of the blade, in the cases of *Joblotia, Tabanus* and *Phlebotomus*, also take part in the enlarging of the wound, acting, however, during the protraction of the blade, for the points of the barbs are directed towards the tip, and do not meet with resistance during retraction. The mandibles and maxillæ, acting together, the former as a saw and the latter as a file, bore a

hole in the skin of the host, and as the hole is deepened the piercing mouth parts are lowered into it either by the movement of the head on the neck or by the flexion of the middle and hind pairs of legs, which results in approximating the body of the fly to the skin of the host. The retraction movement is a more powerful one than the protraction, and we find as a matter of fact, in the forms in which the muscles have been studied carefully, that the retractor muscles are of greater bulk than the protractors, as for instance in *Tabanus* and *Anopheles.*

The process is beautifully demonstrated in the case of *Joblotia.* In this fly the extreme tip is armed on the inner side only with small but stout teeth which do not project from the surface to any great extent, and the first three teeth of this row will be inserted before any resistance is met with in the protraction of the blade. At the level of the third tooth of this set the first of the two sharply pointed teeth on the outer side come into play, and at and beyond this depth both protraction and retraction result in enlarging the wound. When the puncture is so deep that the whole series of seven teeth on the outside and the two distal ones on the inside are introduced into the skin, the larger and blunter teeth on the outer edge come into play, and these are so shaped that they will cut in both directions, having two edges, of which, however, the one projecting backwards is the sharpest and strongest. In *Simulium* the case is much simpler than this, for the armature of the two edges is almost identical, and as all the barbs point upward the movement of retraction is the only one which is efficient in making the puncture. In *Tabanus* the resemblance to a file is very striking, for almost the whole surface of the distal half the blade is beset with powerful spines.

The analogy of the file must not, however, be carried too far. Except perhaps in the case of *Tabanus* and *Simulium,* the blade of the maxilla is not a rigid structure of the same thickness throughout, but is thinned out from the base upwards, and has its teeth set on the thinnest and most flexible portion. This is especially the case in *Ceratapogan* and *Phlebotomus.* In the case of *Joblotia* and *Anopheles,* the thickened internal border is continued to the tip of the blade, but the teeth are on the thin external edge. It might be urged, especially with regard to the mosquito, that the elongated stylets are too slender to bear the strain of this method of action, but the bending stress is not, when one considers the matter carefully, a very great one. On account of the direction of the barbs the greatest part of the resistance of the tissues has to be overcome while the blade is being withdrawn, and it will therefore tend to straighten rather than to bend the blade. The slight flexibility of the blade is in fact an advantage, as it will enable the point to travel to a certain extent

in the direction of least resistance, and if in doing so the blade becomes bent, it will straighten itself on the return, the teeth meanwhile cutting their way through the resistant tissue. The extent of movement is of course a very short one, and is limited to the difference in length between the whole maxilla when the stipes and cardo are in the same straight line and when the stipes and blade form one side of a triangle and the cardo the base. In the most extreme case the excursion of the tip of the blade could not be greater than twice the length of the cardo, supposing the joint between it and the stipes were capable of moving through 180° (Figure 16). The joint between the proximal end of the cardo and the epicranial wall must of course move with the joint distal to it.

It is at first sight a little difficult to believe that these minute cutting organs, so small that even in the largest horse flies they are almost invisible to the naked eye, even though they are provided with such a perfectly adapted armature and muculature, should be able to pierce the thick hide of the larger mammals. And yet they not only do so efficiently, but the larger flies make such a formidable wound that the blood continues to flow after the proboscis is withdrawn, and here, where such species as *Tabanus straitus* and *albamedius* are common, it is by no means rare to see the legs of cattle splashed with blood as if from a bad scratch, as a result of the attack of these flies. The wound made is in fact not a punctured one in the surgical sense, but a lacerated one, and if it happens to involve a capillary of some size the amount of bleeding may be enormous in comparison with the size of the instrument by which it was made. If the piercing parts were simply thrust in it is inconceivable that such minute lancets could draw blood at all.

With regard to the muscles which are concerned in the biting action, it is by no means difficult to believe that they are capable of adequately performing their function without other aid, when we remember the extraordinary rapidity of action of which insect muscle is capable. Marey, quoted by Packard, states that the wing of the fly is capable of making 330 strokes per second, that of the bee 190. This rapidity, probably unequalled in any other creatures, is indeed characteristic of insect muscle, and it seems evident that in the movements of the mandibles and maxillæ of these flies we have another and still more remarkable instance of it, applied in a highly specialised manner. In spite of the very short range of movement and the minute size of the cutting weapons, there is no mechanical reason why a comparatively deep wound should not be made in a very short time, provided the rate of action of the muscles is sufficiently rapid. The abdomen of a mosquito can be seen to begin to distend within half a minute or less from the time it settles down to feed, and it is of course probable that the mandibles and maxillæ continue to act even after the

blood has commenced to flow, and are continually employed in deepening and enlarging the wound as required.

The Sucking Apparatus.

It will be convenient to discuss the sucking apparatus in accordance with its natural division into three parts, the canal in the proboscis, and the buccal and pharyngeal cavities. We may commence with the former, leaving till later the question of the nomenclature of the two cavities which function as sucking pumps.

The canal in the proboscis is formed by the apposition of the labrum-epipharynx and the hypopharynx, the former taking always the larger share in the circumference of the canal. When the labrum-epipharynx is examined in cross section it is seen that it consists of two distinct laminæ, which represent respectively the labrum and the epipharynx. The outer lamina gives its shape to the combined organ, whatever that may be in the individual case, and may be either circular with a gap on the under surface or flattened dorso-ventrally. The upper end of this lamina is attached to the clypeus, and is either quite free from the inner lamina or else more loosely attached than at the distal end. Attached to the internal portion of it, where it reaches the clypeus, there is a well developed muscle which arises from the inner surface of the clypeus. The inner lamina, or the epipharynx, is always circular in outline, or nearly so, and has, like the outer, a gap on its lower or oral side. The two laminæ are attached to one another by the margins which bound the gap, so that they enclose a space in which a small amount of cellular tissue is found, though there is no muscle in this situation comparable with that found in the house fly. The free side of the epipharynx forms the greater part of the food canal, its circumference varying roughly from two-thirds to four-fifths of a circle. The hypopharynx also consists of two laminæ, though they are not so easily distinguished from one another as in the case of the labrum-epipharynx, and no soft tissue can be seen between them. In form the organ is always flat and wide enough to fill up the interval between the lateral borders of the groove in the epipharynx, being in most cases almost as wide as the latter. The epipharynx is always directly continuous with the upper or anterior plate of the first sucking chamber and in a similar manner the upper lamina of the hypopharynx is continuous with the lower plate. The two laminæ are, in fact, simply outgrowths from the stomodæum and are homologous with those of other families of insects. The lower lamina of the hypopharynx arises on the other

hand from the labium, and is therefore quite distinct in its origin from the upper, since it comes from an appendage of the exo-skeleton, and not from the stomodæum.

The most interesting feature of the food canal in the proboscis is the relation of its width to the size of the particles which have to pass along it. Unfortunately it is not possible to make exact measurements of the diameter of the canal in the normal condition of the parts, and any manipulation introduces such a large possibility of error that it is perhaps better to avoid exact figures altogether. In sections prepared by either the combined paraffin and celloidin method or by simple celloidin there is always a good deal of shrinking, and in attempting to measure the width of the canal in fresh or cleared preparations one is met with the difficulty of defining the exact edge of the inner lamina when it is seen in optical section. The width of the channel is only to a limited extent correlated to the size of the fly, and varies from approximately twenty-five microns in the larger Tabanidæ to fifteen or less in Ceratapogon and in mosquitoes; that is to say, it measures from once to twice the diameter of a human red blood corpuscle, it being of course understood that *all measurements are made at the narrowest part of the distal end of the canal* as in many cases there is a gradual widening of the channel from the tip upwards. There are two obvious results of the small size of the channel; in the first place, objects definitely larger than the measurements given will not ordinarily be ingested by these biting flies, a point of some importance to the parasitologist, and which would well repay further investigation, especially with regard to the transmission of filaria by mosquitoes; secondly, if such an object, larger than the canal could conveniently accommodate, were to gain access to the canal, or to become impacted at the opening, which is the narrowest part, there would be considerable danger that the fly would be unable to get rid of it and would consequently die. Now one would think that in such a lacerated wound as that which must be made by the saw and file action of the mandibles and maxillæ there must of necessity be lumps of tissue much larger than can be ingested, and yet it is inherently improbable that nature would allow such an accident to occur. The only conceivable method by which such an impacted object could be got rid of would be by regurgitation, which, since it implies a reversed peristalsis, is a most unlikely event. We must therefore enquire as to what are the possibilities of a defensive mechanism to prevent the ingress into the canal of particles too large to pass down its lumen.

I have already expressed the opinion that the labrum-epipharynx and the hypopharynx can take no part in the making of the wound in the skin, on account of the nature of their attachment to the wall of the head capsule

and of their lack of the necessary musculature. In most of these flies, however, there are certain processes on the distal ends of these organs which certainly bear a superficial resemblance to teeth and have been repeatedly described as such, though I am not aware of any detailed description of the method by which they might be supposed to act. It is just in this situation that one would expect to find a filtering mechanism, and it is worth while to examine these structures in some detail to see if they fulfil the requirements.

Considered with regard to the armature of these organs the flies of this group fall naturally into three divisions, the first including *Simulium*, *Ceratopogon*, and *Phlebotomus*, the second the *Tabonidæ*, and the third the mosquitoes. These will now be examined in detail and compared with one another.

In *Simulium* (figures 15 and 14) the labrum-epipharynx and the hypopharynx, which are flattened and spatulate organs, terminate in gently rounded margins without any point, the middle portion being in fact almost straight. In the labrum-epipharynx there is on each side of the middle line a rather thick longitudinal band of chitin, extending nearly but not quite to the tip, the two bands lying on either side of the food canal. On this band there is a row of fine non-pigmented hairs, somewhat irregularly arranged and extending in an oblique line to the point where the lateral border joins the distal one. They are directed forwards, inwards, and towards the opening of the food canal, and those which are the most proximal in position are a little longer than those at the distal end. At the extreme distal end of the organs there are two sets of extremely minute hooks or teeth, one set on each side of the opening, and projecting beyond the distal margin. On account of their small size and position it is very difficult to be certain of the exact number and arrangement of these structures, which could only be examined satisfactorily in a preparation mounted with the long axis of the organ in the same line as the microscope, and the figure must be taken as approximate only. There appear to be three teeth on each side, each having the shape of a rose thorn, and radiating outwards from their bases. One on each side projects definitely beyond the distal margin. It is somewhat difficult to find a function for these peculiar structures; they cannot be used as cutting teeth, for they are incapable of movement on the labrum, having neither joint or muscles so far as one can see, neither do they appear at all suited for use as a filter. Possibly they are used to fix the organ in position when a suitable depth has been reached. The edge of the labrum-epipharynx on either side of these teeth is very thin and difficult to define in cleared preparations, and is membraneous and probably flaccid; it bears a few minute hairs similar to those on the thickened portion of the surface.

The hypopharynx terminates distally in a border which is parallel to that of the labrum-epipharynx. In this case, however, the organ is chitinous right to its extremity, and is highly modified. The margin on each side of the alivaiy duct is broken up into innumerable minute elongated processes, which form a fine fringe like the frayed edge of a piece of cloth, all the processes being directed distally. This fringe occupies the entire extent of the rounded portion of the distal end, and terminates where the lateral borders become parallel to one another. On the posterior or inferior surface of the hypopharynx there are a few small hairs similar to those on the anterior surface of the labrum, but smaller, and arranged in a loose row near the margin. These arise from the inferior or labial lamina of the organ.

In *Ceratapogon* (figures 6 and 7) we find a similar arrangement, but the serrated border is found on both organs. The labrum-epipharynx is gently rounded at its distal end, and has on each side of the curved distal margin a row of five flattened and blunt pointed processes. These are simply produced by indentations of the margin, and have no thickened bases such as are found in true cutting teeth; they point directly in the long axis of the proboscis and have no fine serrations on their edges; one side of the process is not thinner or sharper than the other. Between the two most internal ones of the two rows there are two other pairs of processes, set on each side of the extreme apex of the organ, where the food canal opens to an exterior. These are rounded, about twice as long as thick, and with slightly constricted necks, which are bent a little backwards so that the rounded ends of the processes hang over the opening of the food channel. The two innermost of the two sides are more distant from each other than any of the other processes, and internal to their bases there is a pair of minute thickenings in the chitin, and proximal to these a medial oblong thickening situated a short distance proximal to the tip of the organ.

The serrated margin of the tip of the labrum-epipharynx is not in the same line as that of the rest of the lateral borders, but is separated from it by a deep notch situated a short distance proximal to the proximal process. This gives the labrum a somewhat barbed appearance. It will be noted in the figures that, if we deduct the width of the slightly thickened margins which project beyond the notch on the two sides, the width of the labrum is almost the same as that of the hypopharynx, and the serrated margin of the former will therefore project beyond the margin of the latter in the natural superimposed condition of the parts.

The hypopharynx resembles the labrum-epipharynx in outline, but, as indicated in the last paragraph, it is slightly smaller. Its margin is also serrated in a manner very similar to that of the labrum-epipharynx, there

being five indentations and five processes on each side. At the point where the salivary duct opens to the exterior there are four small finger-like filaments, which arise from the lower lamina and project distally. The upper or anterior surface of the organ is marked by five longitudinal dark patches, which commence at the bases of the processes in the margin, and pass inwards towards the salivary duct. The appearance suggests that the surface is traversed by oblique longitudinal grooves, with ridges between them, and that the dark patches represent thickened portions of the chitin, but the parts are too small to permit one to be certain of the point.

The parts in *Phlebotomus* are rather simpler. The labrum-epipharynx is produced to a narrower point, the curve of the lateral margins at the distal end being concave rather than convex. The narrowed portion is divided up into a number of minute processes, coarser than those of the hypopharynx of *Simulium*, but much finer than those on that of *Ceratapogon;* the two spine at the extreme apex are rather thicker than those at the sides, and project forwards almost parallel with one another. The hypopharynx has its edge serrated in a similar manner, but the indentations are not quite so deep or so numerous. In its outline the hypopharynx is not quite so much pointed as the labrum-epipharynx, and some of the processes on its margin overlap its edges in the natural condition of the parts.

In these three flies we find, then, that the distal ends of these organs are split up into rows of more or less elongated and pointed processes, varying in shape, but all exhibiting the same general structure, and all directed forwards in line with the proboscis. With the single exception of those on the labrum-epipharynx of *Simulium* they bear no resemblance whatever to biting teeth such as are found in the mandibles and maxillæ of these flies, nor do they resemble those found on the inner surfaces of the labella of the blood-sucking Muscids. Apart from the facts already insisted on, that a suitable motive force and articulation are entirely absent, the nature of the margin, when it is examine ed in a well cleared preparation, is a sufficient indication that it is not primarily intended for cutting purposes. On the other hand, the arrangement is admirably adapted to serve as a filter or sieve, by which large particles can be prevented from entering the canal.

The groove on the under surface of the labrum-epipharynx does not extend to the extreme tip of the organ, but terminates a short distance from it by broadening out into a flattened sheet of softer tissue which is not distinguishable from the anterior lamina, the space between the two being gradually reduced until they come in contact with one another; in other words, the epipharynx does not extend the full length of the combined organ as a separate structure, but is reduced in size and fused with the labrum to form a

more or less flattened and tongue-like end. Normally this lies in front of the flat apex of the hypopharynx, and the opening of the food canal is therefore not a circular one, but a transverse fissure between two superimposed plates. The figure of the ends of the two organs given in Newstead's paper on *Phlebotomus* is most suggestive. He shows that there is a slight interval between the two, caused by a slight forward curve of the labrum-epipharynx and a corresponding backward curve of the hypopharynx. The "teeth" on the former organ are directed slightly backwards, and those on the latter slightly forwards, so as to meet one another and even to overlap to a slight extent, thus filling up the interval which would be left by the curvature of the two extremities. The blood has to pass through the opening guarded by these processes before it can reach the circular portion of the lumen of the canal, and it is evident that the presence of these spines must be a most efficient means of stopping any particle too larger for the lumen from entering it. I have seen a similar appearance in a preparation of *Ceratapogon* amounted on its side, but the evidence of Professor Newstead's drawing is all the more convincing in that it appears to be simply an instance of accurate observation and drawing, for he does not refer in the text to the possibility of the mechanism being a filtering one.

I think it probable that the filtering mechanism provided by these spines is not altogether a passive one, but that the space between the two flattened tips can be varied to a limited extent by means of the muscle situated at the base of the labrum. Probably in the resting condition the two plates are in contact with one another and the spines more or less interlocked, at least in the case of *Phlebotomus;* in other words the mouth of the fly, or rather the prestomal orifice, is closed. When the piercing parts are introduced into the skin as the wound is made, the labrum is raised up a little by means of its muscle, and the potential opening converted into an actual one through which the blood can enter. It is at least very suggestive that the epipharynx and hypopharynx show no sign of fusing together to form a complete tube, in any of these flies, indicating that a certain degree of movement between the two is advantageous for the insect, whereas one would expect that a complete tube would afford greater stability than is provided by the simple apposition of the two organs; since the epipharynx and the hypopharynx are of identical origin, both being outgrowths from the same part of the stomodæum, one would expect such a fusion if a simple tube to function as a food channel were all that were required, and such fusion does actually occur in the upper portion of the canal in the more highly specialised biting flies of the Muscid group.

The *Tabanidæ* (figures 18 and 19) show a different type of apparatus, in which the filtering mechanism is not quite so obvious. Here the labrum-epi-

pharynx is a much stouter and broader organ than the hypopharynx, and it is also slightly longer, so that the tip of the hypopharynx falls a little short of the other stylets. The apex of the labrum-epipharynx is broad and truncated, and the lateral borders are quite free from serrations such as are found in the flies already discussed. On the distal margin there are three sets of tubercles, arising from slightly raised areas, and projecting beyond the distal margin. The two lateral tubercles, which are comparatively large, consist of ten or twelve short stout peg-shaped processes, and the middle set of two rows of five each. Their exact number and arrangement is rather difficult to make out an account of their position, the posterior ones being overlapped by the anterior. The tip of the hypopharynx is distinctly narrower than that of the labrum-epipharynx, and is therefore overlapped by it. The two, however, resemble one another in shape, and, like the labrum-epipharynx, the hypopharynx is devoid of any armature at its sides. In some of the large species, such as *Tabanus striatus*, a distinct flange can be seen at the opening of the salivary duct, and in some preparations the projecting edges of this flange look very like teeth set on either side of the opening. It is easily seen in fresh preparations that they are not teeth, and that the lateral borders of the organ are only very thinly chitinised, so that they do not present well defined edges, but are on the contrary somewhat wavy. The flange at the mouth of the salivary duct bears a few extremely delicate hairs, possibly sensory in function.

In these flies there is therefore no structure which could act as a cutting weapon, and we conclude that they have only to do with the ingestion of food. The tubercles at the apex of the labrum-epipharynx will act as a protecting fringe to prevent the ingress of large particles from the front and sides, but can be by no means so efficient as the well developed fringe found in *Phlebotomus* or *Ceratapogon*. The hypopharynx in this case probably plays the most important part in the mechanism. Its tip and sides are extremely thin and are very easily bent, from which it is justifiable to conclude that in the natural condition they are flaccid. Now Stephens and Newstead, in their description of the mouth parts of *Stomoxys*, make the suggestion that the soft tip of the hypopharynx functions as a valve to prevent the ingress of large particles into the mouth, and I think that the same thing happens in the case of the *Tabanidæ*. In the natural position of the parts the rounded tip of the hypopharynx lies just behind that part of the labrum-epipharynx which bears the tubercles, and since both organs are flattened at the tip they will be normally in contact with one another, except when the labrum is elevated by the muscle at its base. The negative pressure created in the food canal by the dilator muscles of the sucking apparatus will tend to draw the two portions of the sucking tube together, and will act with the greatest effect on that part

which is the most flaccid and the least supported, that is, it will tend to close the prestomal orifice by drawing the apex of the hypopharynx towards the tip of the labrum-epipharynx. The organ is sufficiently rigid to prevent this happening to such a degree as would completely close the orifice, and one must conclude that there is a nice adjustment between the flaccidity of the tip of the hypopharynx and the force tending to approximate it to the labrum-epipharynxe, so that an aperture of the correct size is left between the two.

In the mosquitoes the mechanism by which ingress of large particles is prevented is similar to that in the *Tabandæ*, but on account of the small size and delicate nature of the parts it is much more difficult to follow. The distal end of the labrum-epipharynx (figure 17) varies a good deal in the different forms, but so far as I am aware it never bears any armature which could be used for cutting or piercing. In shape it differs a little from any of the forms so far considered, for the main portion of the labrum-epipharynx is always rounded to the extent of almost four-fifth of a circle, and the transition from this round tube to the flattened tip gives the organ the appearance of being obliquely truncated, something after the shape of a quill pen. In Nuttall and Shipley's monograph on *Anopheles maculipennis* the tip of the organ is shown to be provided with two pairs of fine tooth-like processes, one pair at the extreme point and another pair a little distance behind them. These do not occur in all species of *Anopheles*, and I have not found them in any species of *Culex* which I have examined, even in *Culex concolor*, where they would be easily seen if present on account of the large size of the parts. In a species of *Joblotia* I have found the distal margin indented so as to produce four teeth on each side, the indentations being deep but the spaces between the teeth extremely narrow. There seems to be a considerable amount of variation in the method of termination of this organ, but all forms agree in the essential points, *viz.*, that there are no cutting teeth and that the end of the organ is flattened and fairly thick and rigid.

The tip of the hypopharynx presents a characteristic appearance in the large forms. If one examines the organ in the fresh state under a magnification of at least a thousand diameters and with as small a diaphragm as possible, one sees that the organ does not terminate in a well-defined point as ordinarily depicted, but in a very thin and apparently membraneous expansion, with a gently rounded margin (figure 9). In view of what has already been said with regard to the probable mechanism in the *Tabanidæ* the mechanism in this case will be obvious. The extremity of the hypopharynx lies a little above that of the labrum-epipharynx, so that when the sucking action commences blood can only enter from the posterior aspect, and in doing so will impinge on the soft tip of the hypopharynx and tend to drive it against the more rigid labrum-epi-

pharynx, the stream of blood being aided by the negative pressure in the food canal, which will also tend to draw the two organs together. The entrance to the food channel is not a fixed and rigid one, but varies in size according to the distance between the labrum-epipharynx and the hypopharynx, this being regulated by the muscle at the base of the labrum. The adjustment is a very fine one, for the more powerfully the pharyngeal muscles contract the more will the two parts of the tube be drawn together, and more the valve-like end of the hypopharynx will tend to close the aperture.

A word is necessary with regard to certain minute spines found in the in- ernal surface of the groove of the labrum-epipharynx. I have only found these in *Tabanidæ* and in *Simulium*, but it is likely that they also occur in the other members of the group. They are short, stout, and gently curved structures, arising from expanded and globular bases which lie in the substance of the chitin of the epipharynx, and are seen as clear spaces when the structure is examined in optical section. The base of each of these spines is perforated where it projects into the space between the labrum and the epipharynx, and with careful focussing a fine canal can be seen in the lower part of the free portion of the hair. They closely resemble the spines described in a corresponding situation in *Stomoxys* by Hansen and by Stephens and Newstead, and one is inclined to regard them, from their situation, as organs of taste, though of course there is no direct evidence as to their function. Possibly it may be through them that communication between the prestomal orifice and the muscle of the labrum is established for the purpose of regulating the flow of blood. Their occurrence in such a widely separated flies as *Simulium* and *Stomoxys* is suggestive.

The mechanism of the labium appears to have escaped the notice of workers on this subject. It is generally stated that when the mosquito feeds the labium becomes bent backwards like a bow, and the labella separated to allow the piercing parts to pass between them, but no mention is made of the forces which bring about this change in position, and one is left to assume that the labium is simply pushed back because it cannot enter the skin. The process can be readily watched in the mosquito, and is faithfully depicted in Nuttall and Shipley's drawing. In all the other flies without exception the same thing must take place, since the labium and labella are always long enough to conceal the mouth parts in the condition of rest. There is no reason to suppose that there is any such haphazard bending as that indicated above, for the labium has its intrinsic muscles, some arising within the head capsule and some within the cavity of the organ, which are inserted into its integument at the distal end and into the labella. These are familiar from the many diagrams of the cross-section of the proboscis

of the mosquito, and are of course figured in the classical papers of Meinert and Hansen. In most Nematocerous flies the labium and labella are separated from one another by a loose joint in which there are lateral transverse bars of chitin, very conspicuous but not described in detail in the mosquito, which are probably homologous with the furca in the muscid flies, and some of the muscle fibres can be traced to these in the large mosquitoes. We have here all that is required for the retraction of the labium and the eversion of the labella which can be seen to take place when the fly feeds. The muscle fibres arising within the cavity of the labium and inserted into these transverse rods evert the labella to allow the piercing parts to enter the skin, exactly as is the case in *Tabanus* where the labella are large and important structures with a function of their own with regard to feeding. The retraction of the labium and the bent position it assumes are the result of the contraction of its muscles and of the peculiar structure of its wall. The mentum of the mosquito is a long chitinous gutter, straight or slightly curved, and of fairly uniform diameter throughout; its anterior open side is filled in by a soft membrane homologous with the labial gutter of other flies. The chitin of which it is composed is not, as generally represented, a continuous sheet, but is in its upper portion composed of a large number of separate narrow transverse plates, set very closely together and united by the membraneous ground work. These are very minute, and are only revealed by the examination of well-cleared preparations under a high magnification. They are found at just that portion of the labium which is bent acutely when the piercing parts are inserted into the skin, and the arrangement is, of course, one with which one is familiar in other situations in which a certain amount of rigidity has to be combined with flexibility.

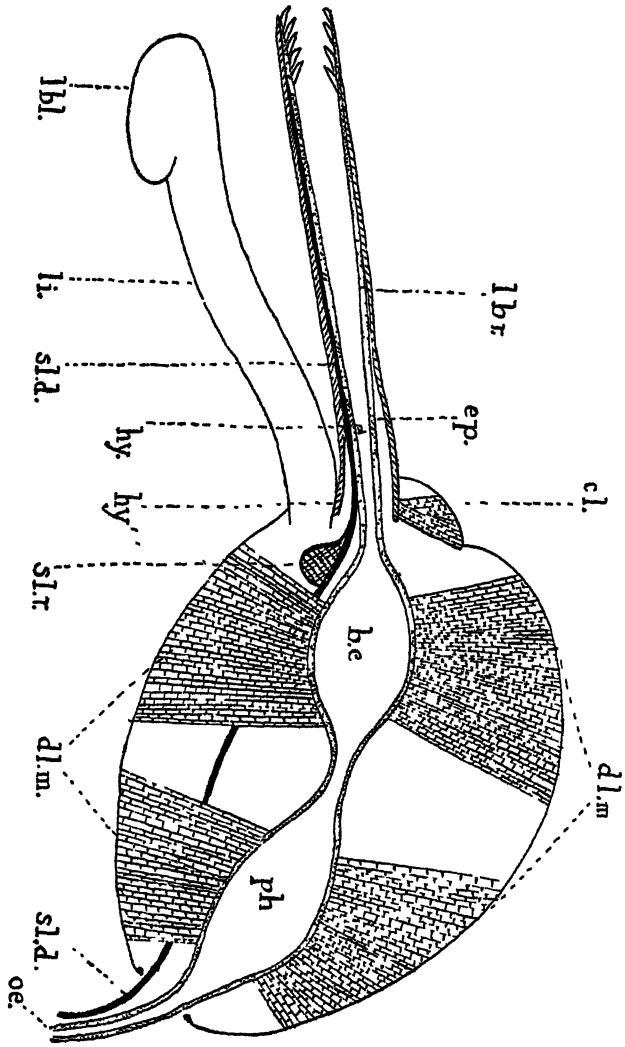
The Sucking Chambers.

The nomenclature of the sucking apparatus in the Diptera is unfortunately in a most confused state, and it will be well before going further to fix a terminology and to point out the significance of the terms employed by different writers. It is agreed by all that the sucking apparatus is formed from the first part of the stomodæum, and is therefore an invagination at the anterior end of the fly, lined with chitin which is continuous with the exoskeleton. In all the Orthorrapha this invagination is dilated into two chambers, each of which, in the species which have been examined closely, is provided with a set of muscles which pass between the outer sides of the walls of the chamber and the walls of the head capsule. By means of these muscles the chambers can be dilated, so that their potential cavity becomes an actual one, into which the fluid food is sucked by a simple pumping action. The two

chambers appear to be always separated by a narrower channel, which may be surrounded by a sphincter muscle, so that they work alternately, the posterior chamber drawing the blood from the anterior one, and passing it onwards into the alimentary canal. It is with regard to the respective names of these two chambers that the confusion exists, and this has arisen chiefly through the differences in degree of development of the two in different families, and to attempts to follow too closely the terms employed in general anatomy. Meinert, in his description of *Tabanus*, termed the first of these, which in that family is rather more prominent than the second, the pharynx, and then divided the succeeding part into the first and second parts of the œsophagus, the first part being a large and dilatable chamber, the second a simple tube passing through the brain to the neck. In the mosquito it is the second chamber which is the most conspicuous, and this is universally known as the pharynx, at least at the present time, subsequent to the description of Christophers. Nuttall and Shipley term the first portion the buccal cavity and the second the pharynx in the mosquito, and I think it would be of advantage to retain these terms throughout the group. The word œsophagus is chiefly used in zoological nomenclature for a simple channel, and there is no special advantage in retaining it to signify a part of the sucking apparatus. This nomenclature has the advantage that it is equally applicable to the Cyclorraphic Diptera, in which there are also two parts to the apparatus, only one of which, the upper one, is a functional pump. It must be remembered, however, that that pharynx in *Tabanus* and in the mosquito, the two most divergent members of the group, possess this difference, that they are on opposite sides of the brain, the pharynx of the former—the first part of the œsophagus according to Meinert—being anterior, and that of the mosquito posterior. In what follows, then, the first chamber will be termed the *buccal cavity*, corresponding to the pharynx of Meinert and Dimmock, and the second the pharynx, corresponding to the first part of the œsophagus of the same authors, and homologous with the fulcrum in the house fly as described by Kraepelin, and the pharynx of Lowne. The simple tube which connects the pharynx with the alimentary canal in the thorax may be termed the œsophagus. The duct which unites the buccal cavity and the pharynx hardly needs a special name.

It is to be understood that this nomenclature has no precise embryological significance, and that the pharynx in one fly is not necessarily strictly homologous with that of another. We may imagine that in a very primitive insect of this type the whole of the outer wall of the stomodæum would be united with the wall of the head capsule by strands of muscle fibre, so that it formed one continuous dilatable chamber, in which a sucking action

could be produced by the peristaltic contraction of the muscles, the anterior one contracting first, and then relaxing, so that a wave of dilatation



TEXT FIGURE 2.

Diagram of the sucking apparatus of the orthoraphic biting flies. lbr., labrum. ep., epipharynx. cl., clypeus.

hy., hy'., the anterior and posterior laminæ of the hypopharynx. sl.d., the salivary duct. li., labium. lbl. the labella. sl.r., the salivary reservoir.

b. c., the buccal cavity. ph., the pharynx. dl. m., the dilator muscles, passing from the wall of the head capsule to the sucking chambers. oe., the œsophagus, entering he neck.

passed along the chamber, carrying the food with it onwards to the digestive portion of the canal. In course of time, as the various genera were differentiated from one another, certain portions of the muscle disappeared and the chamber became divided up, until in the present forms two main dilatations were left, a small portion of the stomodæum in the head remaining

as a simple duct. The condition found in the different families depends simply on the particular portions of the primitive chamber which have retained the original character, and it is quite possible that these are not always the same. One is not perhaps justified in speculating further on this subject in view of the little that is known of the larval characters of these flies, but it is interesting to note in passing that there are points which suggest that the pharynx of the mosquito is developed from a part of the stomodæum much posterior to that from which the pharynx of *Tabanus* arises, although the chamber here referred to was regarded as the first part of the œsophagus by Meinert. In the first place, the second chamber of the mosquito is posterior to the brain, while the corresponding chamber in the *Tabanidæ* is anterior. In *Tabanus* we find also that there is a well-defined pair of muscles, the retractors of the œsophagus, which run from the posterior wall of the head capsule in the neighbourhood of the occipital foramen to the œsophagus, and though their function is probably correctly indicated by their name, they represent a portion of the once continuous band which united the whole of the wall of the canal to the head capsule. They correspond in position, with regard to the brain, to the large and powerful dilator muscles of the pharynx of the mosquito, and it certainly looks as if the part of the canal to which they are attached is homologous with the pharynx of the mosquito.

The Mechanism of the Sucking Pumps.

In the numerous descriptions that have been published of the pharynx and its muscles, no account seems to have been taken of the necessity that exists for some method by which the distended chamber can be closed again, and the plates once more brought in contact with one another in readiness for the next contraction. It is generally assumed that the recoil of the plates takes place by virtue of their elasticity, an assumption that does not seem to be justified by the facts of the case as far as they are known. Chitin is certainly to some extent flexible when it is in thin sheets, and the chitinous mouth parts when bent will as a rule return to their original shape, but it by no means follows that the elasticity of the chitinous plates of the sucking chambers is sufficient to bring about their return, for it must be remembered that such a degree of elasticity would have to be overcome by the dilator muscles when the chamber were expanded. It is of course as difficult to prove that the plates are not elastic as it is easy to assume that they are, and I will not go further than to say that the assumption is an unnecessary one. Let us consider what must happen when the chamber is dilated. In the first place, if the head

were entirely separated from the body, the total contents would be increased, and either some of the cranial contents would have to be compressed or the capacity of the head increased by distension; the difference in size between the cavity of the pharynx of the mosquito when it is empty and when it is full is considerable, when compared with the total size of the head. The only compressible substance in the insect head is the air in the air sacs, and the only substances which can be displaced from the head by simple pressure are the air in the air sacs and the blood in the hæmato cœle of the head. If these are displaced by the expansion of the sucking chamber they will pass through the neck and increase the total contents of the body. There are therefore two possible ways by which the chambers can be emptied after dilatation, *viz.*, by blood pressure or air pressure. Of the two the latter is the more likely, both on account of the structural peculiarities of the head and by reason of the analogy of the method by which the retractile proboscis of *Musca* is known to be thrust out. The head of the fly, and particularly of these blood-sucking flies, contains a remarkably large amount of air, contained in air sacs with relatively thick walls—very thick in the case of the *Tabanidæ.* The air in these sacs is in communication with the rest of the tracheal system by means of tracheæ which pass through the neck, and so with the thoracic spiracles. That the insect is capable of distending the air sacs of the head by means of respiratory movements we know from the case of *Musca,* so thoroughly studied by Kraepelin, and I think that the dilatation of these sacs offers a far more rational explanation of the means by which the plates of the pharynx and the buccal cavity are brought together, than the assumption that the chitin has of itself sufficient elacticity to accomplish it.

The Intracranial Tunnels.

In all the flies of this group there exists a pair of hollow tunnels which pass through the lower part of the head from front to back, and open on to the anterior and posterior surfaces. They have been described and figured in *Anopheles* by Nuttall and Shipley, and by myself in *Hæmatopota.* Similar tunnels occur also in *Chironomus* (Miall and Hammond) and in *Asilus.* They act as supporting buttresses to counteract the tendency of the dilator muscles of the sucking apparatus to pull the walls of the cranial cavity together, and, as I have pointed out in connection with those of *Hæmatopota,* the fact that they are hollow is in accordance with the mechanical principle that a hollow cylinder is stronger, weight for weight, than a solid rod. They also act as an additional surface for muscle insertion, and several muscle bundles can be traced to their posterior ends. The anterior end of the tunnel opens in all

s just below and at the outer side of the antenna, and the posterior a little ront of the occipital foramen. The interesting point about these structures ıeir constant occurrence and their connection with the sucking apparatus.

The Oesophageal Diverticula.

It does not appear to be fully recognised that the presence of an œsopha-ıl diverticulum is a constant feature in Diptera, and that the form in which ɔccurs in the mosquito is merely a modification of a structure well known t only in this order but throughout the whole class *Insecta*. A good deal of ɔ confusion is possibly due to the loose way in which many names, more or s applicable, are used for the different forms in which the structure occurs. any of them are open to objection; probably it would conduce to clearer ideas the subject if the term "crop" were adopted for all, though it is of course ther too late to attempt to change the term in such common use in connec-ɔn with mosquitoes. The words "œsophageal diverticulum" are, however, mewhat misleading. The real relations of the two parts are best seen in a ngitudinal section of the anterior part of the thorax of a Tabanid, or in a ries of transverse sections. The duct of the diverculum passes in a straight ıe backwards through the neck, lying between the salivary glands; in front is directly continuous with the œsophagus, and there is nothing to indicate here the one ends and the other begins, as they are precisely similar in the ructure, and form one continuous duct extending from the intracerebral ɑrt of the œsophagus in the head to the small sac-like diverticulum in the ɔcond or third segment of the abdomen. At a point a little distance be-ind the inlet of the thorax the proventriculus is seen lying below the duct nd between the salivary glands, and it has an aperture on its upper surface y means of which it opens into the lower surface of the duct. The junction etween the two is therefore at a right angle to the line of the gut, and it is, n the *Tabanidæ*, surrounded by a few circular muscle fibres which may func-ion as a sphincter muscle. It is clear that in view of this it is literally ncorrect to speak of the sac as a diverticulum of the œsophagus. The term ' sucking stomach" is open to the even more serious objection that it is not a tomach, in the sense of an organ in which digestion takes place, and that it is ıot a sucking organ. On the whole the term crop is the most applicable of ɑny of he words in use, as it indicates the function fairly closely, and has the ɑdvantage of emphasising the homology between the apparently different structures in the mosquito and the house fly.

The crop is primarily the chamber into which the blood first flows from the pharynx, and is intended, no doubt, as a reservoir to contain the food until the digestive portion of the midgut is ready for it. The different degrees of

development which it attains are dependent on the amount of food the midgut can deal with at one time. In a full-fed mosquito killed immediately after feeding one finds the three divisions of the crop all filled with blood, and very little in the midgut, while in a horse fly the crop is empty and the midgut distended with blood. In the former case we may regard the crop as a true reservoir, as was pointed out by Nuttall and Shipley, while in the latter the function appears to be merely to pass on the blood slowly from the pharynx to the midgut. The wall of the crop is composed of a very fine basement membrane and an interlacing network of delicate muscle fibres, and the degree of the development of the muscle gives one support to the observations made on the fly in dissections. In the *Tabanidæ* the muscle fibres are very well developed, forming a network which can easily be seen in unstained preparations, and the sac is thus able to pass on at once the whole of the blood received by it to the gut, contractions of the wall of the sac following relaxation and emptying of the pharynx. I have dissected for various purposes several hundreds of Tabanids of various species, and at varying times after feeding, and have never found fresh blood in the sac in any case. In flies killed immediately after feeding one often sees the wall of the sac displaying rather rapid peristaltic movements, such as would result in driving the blood out of the sac and up the tube into the proventriculus. In flies killed some time after feeding the sac is either empty or contains a few granules of blood pigment. In the *Tabanidæ* the crop is therefore to be regarded as functionally a part of the sucking apparatus, its task being to receive the blood from the sucking pharynx and to expel it again into the midgut, while in the mosquitoes it is a true reservoir, retaining the blood at the time of feeding and passing it on to the gut as it is required later, the contractions not necessarily taking place immediately after the blood is received and not being correlated with the contractions of the pharynx.

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Description of Plate.

The figures were drawn with the aid of a camera lucida.

Figures 1 to 15 are on the same scale as that to the right of figure 1 and figures 17 to 19 on the same scale as that at the right lower corner of the plate. The divisions in the scales in each case represent hundredths of a millemetre.

Figure 1. The edge of the maxilla of Simulium.
Figure 2. The edge of the mandible of Simulium.
Figure 3. Ditto Ceratapogon.
Figure 4. Ditto Tabanus.
Figure 5. Ditto Anopheles.
Figure 6. The distal end of the labrum-epipharynx of Ceratapogon.
Figure 7. Ditto hypopharynx do.
Figure 8. Ditto Maxilla do.
Figure 9. Ditto hypopharynx of Joblotia.
Figure 10. The edge of the maxilla of Tabanus, showing some of the teeth.
Figure 11. Three red cells and a large mononuclear cell of human blood drawn for comparison of size.
Figure 12. The distal end of the maxilla of Phlebotomus.
Figure 13. The distal end of the maxilla of Joblotia. The curvature is probably an artifact, *vide* page 11.
Figure 14. The distal end of the hypopharynx of Simulium indicum.
Figure 15. Ditto Labrum-epipharynx do.
Figure 16. To indicate the extent and direction of the movement of the maxilla in Tabanus Diagramatic.
Figure 17. The distal end of the labrum-epipharynx of Joblotia.
Figure 18. Ditto hypopharynx of Hæmatopota.
Figure 19. Ditto labrum-epipharynx do.

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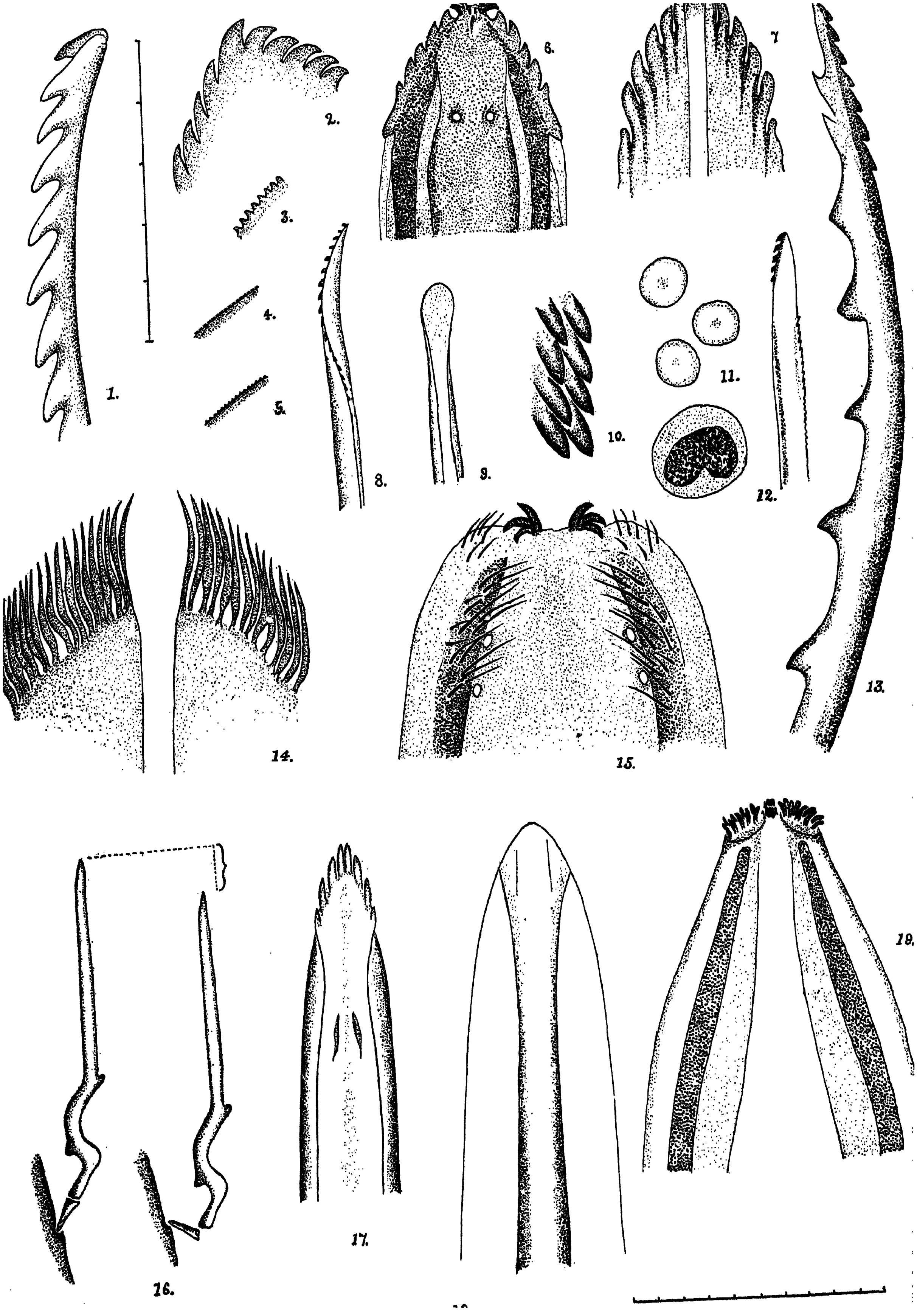
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